Salt as a non-food: to what extent do gustatory perceptions determine non-food vs food choices?

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Most physiologists believed for several years — and some of them still believe — that taste perception is limited to four or five primary taste perceptions (salty, sweet, sour, bitter, and eventually umami), with the implicit idea that a pure chemical such as sodium chloride does elicit what could be named a 'pure taste'. However, the hypothesis of a small number of basic tastes does not fit with recent electrophysiological records on primates taste nerves and on the neurones of primary and secondary taste cortex (Rolls, 2004; Scott and Plata-Salamán, 2004). The taste signals transmitted by taste nerve fibres, are complex and involve, in the brain, a combination of various neurones flashing simultaneously, even in the case of the response to a solution of a simple compound such as sodium chloride.

In the same vein, the present utilisation of salt in cooked foods throughout the world led several scientists to consider that salt is a basic and compulsory part of the human diet and that our ability to perceive the salty taste is an adaptive trait that evolved with our primate ancestors. Of course, the nutritional requirements for a balanced diet include sodium chloride (Randoin *et al.*, 1985), as well as several other salts, most of them in small but compulsory proportion of the global food intake. But the evolution of the primate taste system must be understood according to fossil records, with the help of the observations and experiments on the extant primate species, and according to adaptations to various environmental conditions (Hladik *et al.*, 2003; Hladik and Pasquet, 2004). Such considerations, that we are going to present here, shed a new light on taste perception, and especially salt perception that can be considered as a side effect taste evolution.

These considerations are also related to the issue about the limit between foods and 'non-foods' for humans. Among field observations of anthropologists and primatologists, the practice of geophagy (eating earth) has been described and often explained as a search for sodium chloride. The analysis of the clay or other type of earth eaten by non-human primates have shown that, in most instances, the salt or the salty taste is not a relevant parameter determining intake. However, clay could be a complementary part of non-human primate's vegetarian diets, according to its role in plant detoxification (Johns and Duquette, 1991). In humans, further considerations (presented by other authors of this volume) show evidence of non-nutritional factors determining geophagy. Accordingly, while clay is a true part of the diet of non-human primates, it is a 'non-food' for humans, and, in this context, sodium chlmoride could also be considered as a kind of 'non-food' for the humans, who presently consume salt in such large amounts (nutritionally useless) that the risk of cardio-vascular diseases might be significantly increased.

The salty taste and the status of salt for humans

Since I am not a cultural anthropologist, my own data related to the status of salt in various populations are limited to a few studies for which I was working in an interdisciplinary programme together with my colleagues anthropologists. These studies, however, focused on the variability of taste sensitivity, provided the opportunity to investigate the perception of peoples adapted to contrasted environments, such as the Inuit of Greenland and the Aka Pygmies of the equatorial rainforest.

Interestingly, salt can be perceived either as a distasteful or as a very pleasant taste, when comparing two populations living in drastically different environmental conditions, but who share a quite comparable diet including the highest proportion of animal protein observed throughout the world. For the Inuit, who make their living by hunting seals and other large marine mammals along the coast of Greenland, the preferred food is boiled meat with the lowest salt concentration (using melted ice carefully selected out of freshwater icebergs). When an European explorer, at the beginning of the 20th century, offered salted fish to the Inuit, they try to eat a piece but immediately spat out the bite with surprise and disgust (P. Robbe, 1994). In contrast, in the African rain forest, salt has been a classical gift from early explorers, and still is appreciated by Pygmies who crave for salty foods. For the Aka and Baka Pygmies, besides meat of wild game, both salt and sugar are prestigious foods. They do like salt as much as all sweets, especially the honey from wild bees that is one the highest ranking gift (B. Robbe and Hladik, 1994). Thus it is not quite surprising, in this cultural context, that the same word can be used for the taste of sugar and that of salt (Hladik, 1996).

We had recently the opportunity to compare taste perceptions in another cultual context, that of the Susu of Guinea who live along the coast, where they devote a large part of their activity to extracting salt out of the salty mud of mangroves, using a sophisticated technique of boiling concentrated salty solutions. The process of extraction leads to a soft white powder, designated as ‘female salt’ and to crystalline concretions named ‘male salt’. Both female and male salts, that may content various salts besides sodium chloride, are perceived as different as regards to tastes and virtues. We just carried on a few taste tests to get comments about these salty tastes and those, for example of very acid fruits (*Salacia senegalensis*) or of the strongly astringent immature yellow fruits of *Phenix reclinata*, and all other known tastes. In this Susu cultural context where salt is so important, when the taste of pure salt was compared to other tastes, in order to find differences and partial similarities, it appeared to be perceived as a very strong taste, as strong as that of the hot pepper.

Thus, such cultural contexts may drastically influence the perceptions and appreciation of the various compounds of foods and non-foods. However, to show how far this can determine a limit between foods and non-foods, we have to consider some of the functional aspects of the taste responses, especially according to the activation taste bud cells on the tongue surface, the connections of peripheral taste nerve fibers to brain taste areas, and the links to other brain parts, as described by Rolls (2004).

Salt among other taste stimulations

In Humans, the level of taste sensitivity — allowing comparisons between individuals and population — can be assessed through simple and reliable tests (Simmen *et al.*, 2004). We have measured taste recognition thresholds with diluted solutions of sugar, bitter substances, organic acids and tannins, together with salt solutions, allowing to determine what is the dilution actually perceived during blind tests. Each of the series of solutions of these purified substances is not devoted to a 'basic taste'; rather it can be considered as a kind of probe allowing to find the limits of efficiency of the complex taste signals, in relation to genetically determined capacities of individuals within each population.

According to the results of such measurements we could compare the responses to salt of the Inuit to that of various groups of Pygmies, as well as to those of sub-samples of the populations of Africa, Europe and Asia. The extreme sensitivity to salt of the Inuit (Hladik et al., 1986) was quite remarkable as compared to that of other population sub-samples, especially those of various countries of Europe investigated during a program of the European Union focused on health and food choice (Gerber and Padilla, 1998). Although most aversive responses to salt of the Inuit are obviously culturally learned, the biological peculiarity of this population in terms of taste sensitivity appeared as an adaptive trait. It helps to prevent the excessive intake of sodium which could result of the large quantity of drinking water (5 to 6 litres per day) characteristic of the protein-rich diet that triggers renal elimination of the products of catabolism. If the ice collected from icebergs (melted for drinking water) would have been polluted by sea water, the excess of sodium intake would have been hazardous, in terms of cardiovascular risk, hence the advantage of a trend towards a high sensitivity to sodium chloride (Robbe and Hladik, 1994).

These measurements of the taste responses could also show the relationships between taste responses to various compounds as a global shaping of the taste system of *Homo sapiens* (Hladik and Pasquet, 2004). Figure 1 shows this global result after using all individual data in a paired-sample correlation analysis: the correlation between the perception of two compounds shows a partial similarity between the signals (i.e. a part of the taste receptors and taste fibres are common to both perceptions). Concerning the sugars fructose and sucrose there is an obvious similarity shown by a short distance in this diagram. Concerning sodium chloride as well as citric acid, the distance to sugars is fairly long, but this diagram shows that a part of the receptors and fibres are common to these perceptions. Finally, for bitter substances such as quinine, and the strongly astringent plant secondary compounds such as tannins, the distance to sweet perception is large, thus implying a quite different set of taste receptors.

However, the intermediate place of salt perception, thus sharing some of the taste fibres involved for sweet and bitter substances, involves a peculiar status, and may partly explain why salty taste is considered either as pleasant or as distasteful.

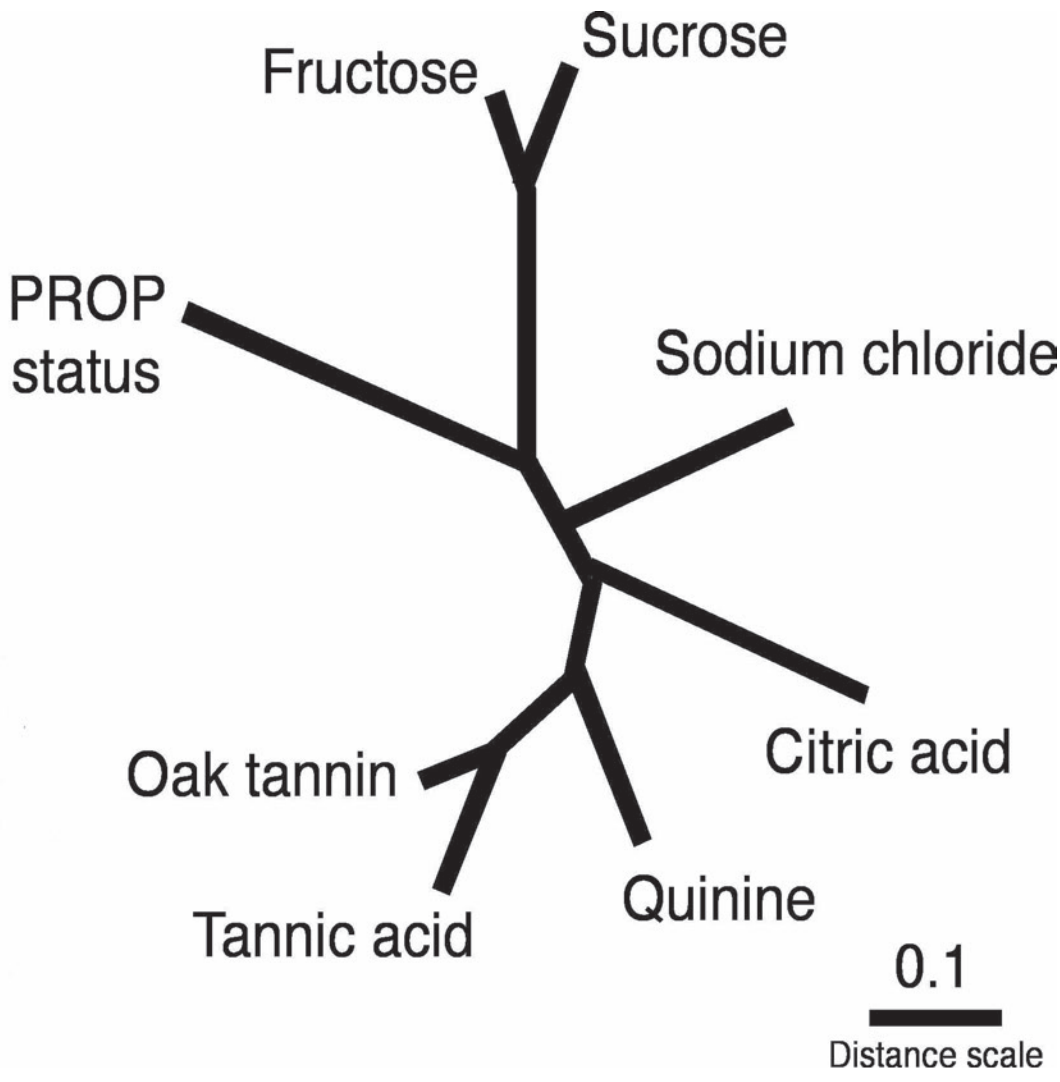

Figure 1 — This additive tree shows correlation among recognition tastes thresholds for various compounds (including the propylthiouracile, PROP), in a total of 412 human subjects from population sub-samples of Europe, Asia and Africa.

The evolutionary background of taste perception

In order to understand the origin and the evolution of the ability to perceive the tastes of various compounds of the foods available in different environments, we must compare taste sensitivities of human and non-human primates, although the measurement of taste responses with lemurs, monkeys and apes necessitates a quite different technique (Simmen *et al.*, 2004). It is remarkable that, using such totally different techniques (especially recording signals on the taste nerve), a global pattern of the primate taste system appears, quite similar to that constructed with the human responses. When constructing a tree of correlation (Figure 2), using the signals recorded on taste nerve isolated fibres by Hellekant and Danilova (2004), the analogy with the previous tree

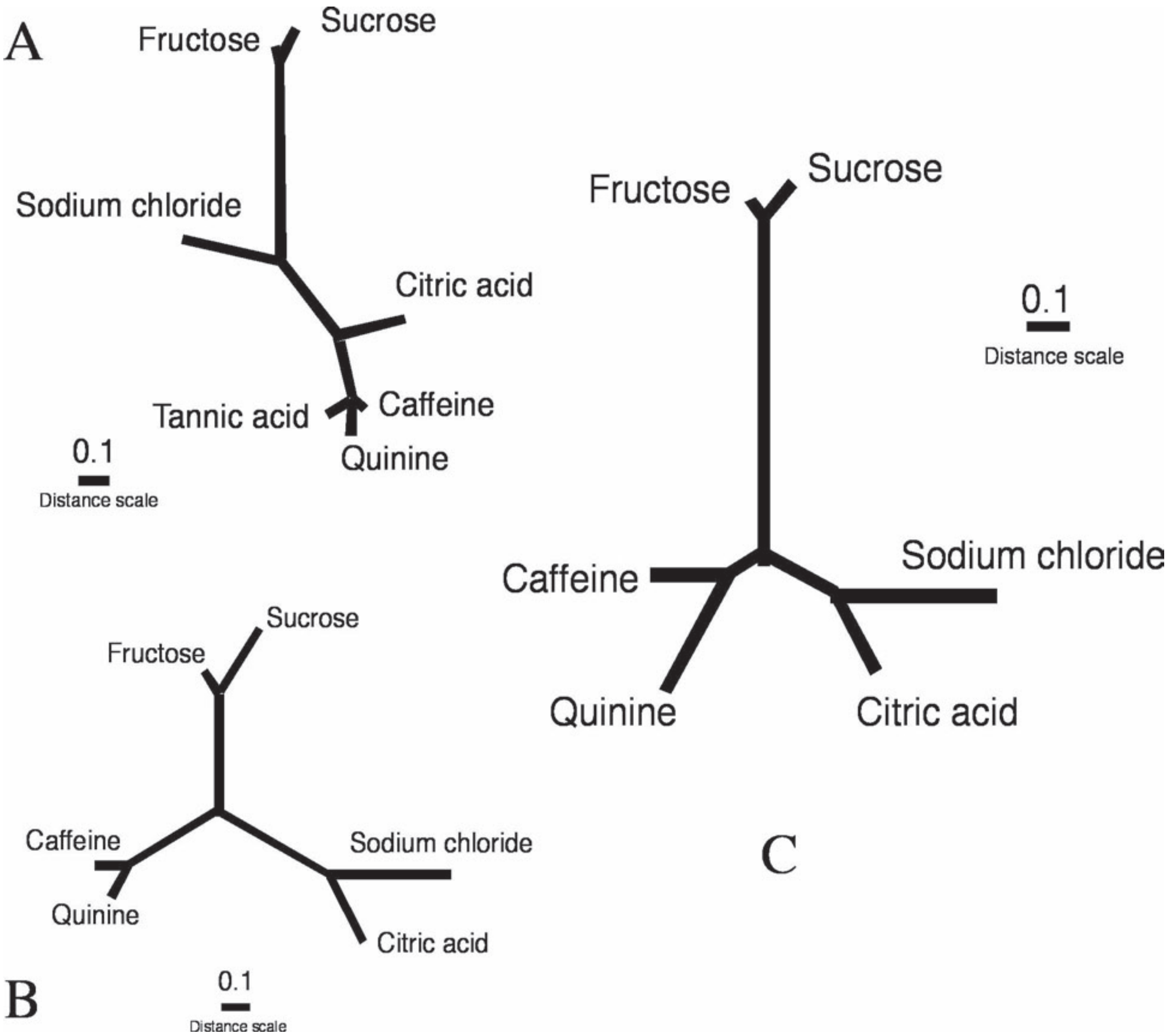

Figure 2 — Additive trees, showing the correlation among responses of isolated taste fibres (data from Hellekant et al.) after stimulation with solutions of various compounds applied to the tongue of non-human primates:
A — The marmoset (*Callithrix jacchus*)
B — The rhesus macaque (*Macaca mulatta*)
C — The chimpanzee (*Pan troglodytes*)

constructed with correlation between the human taste thresholds, the dichotomy appears between the responses to beneficent compounds (mostly sugars) and the responses to potentially harmful compounds such as tannins and alkaloids. Some variations between primate species concern salts, especially the response to sodium chloride which perception might be closer to that of acids, tannins and quinine, most of them potentially harmful. In most instances, if concentration of the tested solution is high enough, salt is avoided by non-human primates and perceived by humans as a bad taste.

In all primate species including humans, the gusto-facial reflexes reflect this dichotomy of the taste system. In new-borns, whereas the contact with the tongue of sugar solutions elicits relaxation of all facial muscles and facilitate swallowing, the contact with bitter compounds such as quinine triggers an immediate contraction and spitting (Steiner *et al*., 2001). Such reflexes, obviously adaptive, are most probably the result of the long lasting co-evolution history (during the Cenozoic Era) of the primates and the angiosperms providing fruits with a pulp rich in sugars, in various environments where previous selective pressure have maintained plant species resisting to herbivorous invertebrates and vertabres, thanks to the presence of secondary compounds such as alkaloids ans tannins (Janzen, 1978). The taste thresholds for all these beneficent or potentially toxic compounds vary among primate species, in relation to the content of plant species in various environments (Simmen and Hladik, 1993)

Concerning the taste of salts, especially that of sodium chloride, the natural setting is totally different, since salt concentrations in food plants are far below the recognition thresholds of primates species, including humans. Accordingly most primates (except some rare species living along the sea shore) never experienced the salty taste thus, there is no evidence of any selective pressure allowing selection of food plants, or non-foods such as pieces of earth, according to sodium content. This is true for forest primates, as well as for the first human populations if we consider the data available on various natural environments. For instance, in the diet of a leaf-monkey, the gray langur (*Semnopithecus entellus*), the mineral content of food plant is enough to supply nutritional riquirements, but at a very low concentration (generally below 1 millimole in the juice of most plants). When we compared this content to that of the clay which is often ingested (especially in pieces of termite mounds), we found an even lower mineral content in the clay (Hladik and Gueguen, 1974), showing that, in that case, geophagy was not determined by the presence of salt. Most salts nutritionally available (especially sodium chloride) are not detectable by primate at such a low concentration.

Our hypothesis was that the clay eaten by leaf-monkeys — and by most primates extensively feeding on foliage — could play a role in detoxification by its adsorbing activity. This activity of clay, especially adsorption of the tannins and other anti-feedants or toxic substances, has been experimentally demonstrated by Timothy Johns and Duquette (1991). Accordingly, the ingestion of pieces of earth rich in clay could be essential as providing a useful supplement of the diet, at least for several species of non-human primates.

Considering that there is no craving for salt, and that sodium chloride is not detectable by the primate taste system in the foodstuffs of most natural environments, we may wonder why we can actually perceive a salty taste. Obviously, the extant species of non-human primates have no experience of the taste of salt and there is no evidence of a selective pressure exerted during the whole Cenozoic Era that could have selected

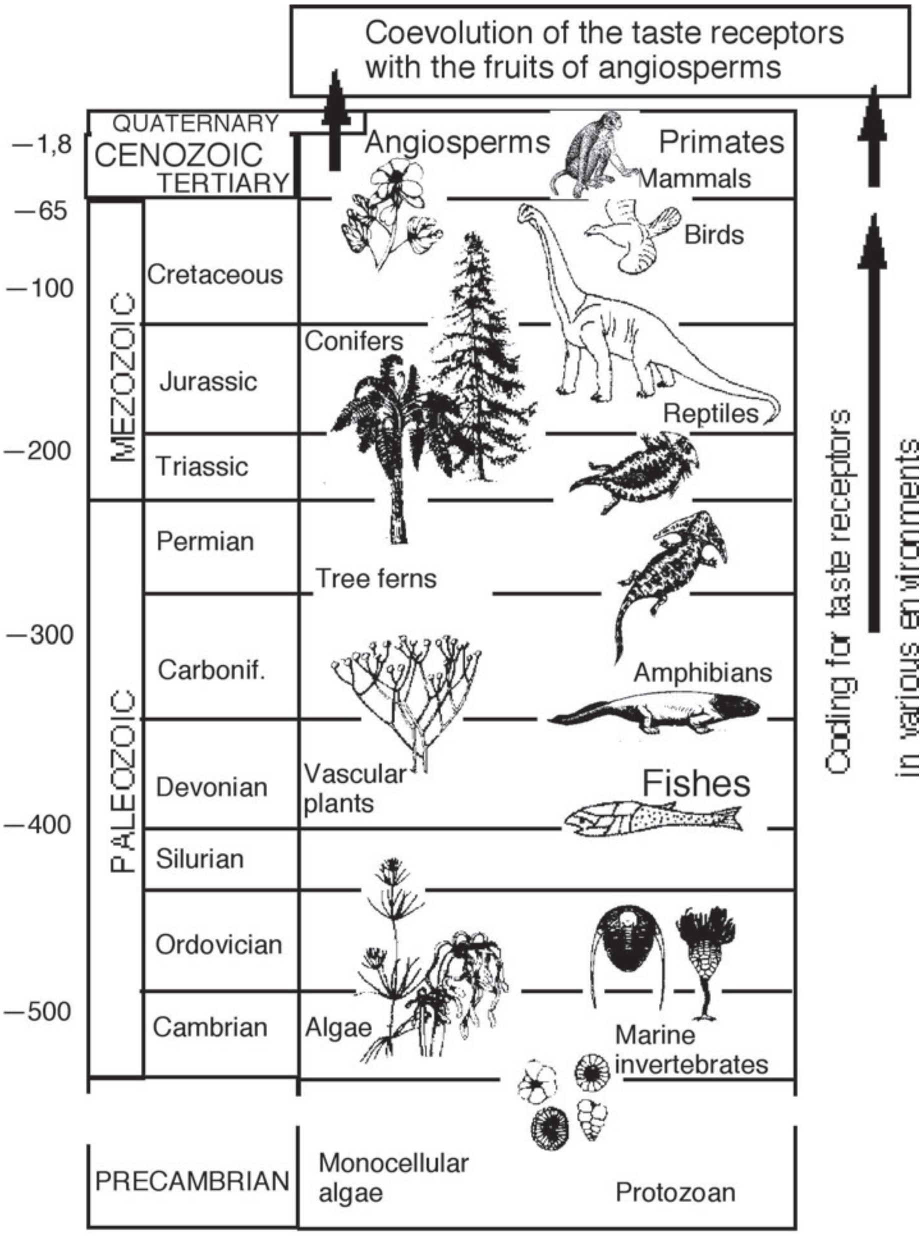

Figure 3 — The parallel evolution of plants and animals (age in Myears), showing coevolution between the primate taste system and fruit composition of the angiosperm species during the Cenozoic Era. Primate taste receptors are derived from those of aquatic vertebrate ancestors which evolved as amphibians reptiles and mammals, with chemoreceptors being exclusively located inside the oral cavity. Genes coding for taste receptors were selected according to successive changes in the biochemical environments in which terrestrial vertebrates evolved.

the primates best responding to sodium chloride. The concentration of salt eliciting a response in a lesser mouse lemur, or in a macaque are in the same range as the median thresholds that we found in various human populations (Hladik and Simmen, 1996), reaching about one hundred times the concentrations observed in food plants.

However, everyone knows that salt can be licked by mammals including primates, such as *Lemur catta* that we observed in the south of Madagascar. But this always occurs in peculiar conditions: locally it could be due to the presence of a wall with salt exudates. Why primates actually perceive salts when the concentration is higher than in food plants?

We have indeed to consider the evolutionary history of vertebrates, which is not restricted to the relatively recent co-evolution of the Primate Order in parallel with the angiosperms that evolved the juicy fruits rich in sugars. The positive taste response to sweetness benefited to plant seed dispersal, and we are among the primates for which sweetness has been selected. However, before this evolutionary venture, the first vertebrates were fishes that had to cope with salted or freshwater (as illustrated in Figure 3). Some of the extant fish species (such as the minnow, *Phoxinus phoxinus*) are still able to perceive sodium chloride and other salts through their skin, covered with taste buds quite similar to those lining our tongue. And they are able to detect very low concentrations (lesser than one millimole).

The taste buds responding to various substances, notably to the tannins, that evolved with the first terrestrial plant species, have been restricted to the inside the mouth of reptiles, then birds and mammals. Complex combinations of the taste receptors allowing to respond to substances more sophisticated than pure salts, led to the complex taste signal, according to genome " tinkering " with old genes during the various phases of vertebrate (and primate) evolution. Finally, during the period of co-evolution of primates and angiosperms, tastes responses have been adapting to sugars and other more complex substances, but, of course, several taste receptors have kept their original ability to respond to salt.

Is salt a non-food?

Tastes of astringent or bitter compounds, even though the content is low, are actually perceivable by all primates in several non-foods such as the barks consumed by the chimpanzees observed in Uganda by Sabrina Krief (2004). When these non-foods are used, there is a reversal of the normal behaviour than can provide a beneficial effect due to activity against parasites of low amounts of active compounds. This is exactly the opposite of pica maladapted use. All these type of non-foods can thus be considered as part of the diet.

Conversely, the utilisation of cooked salted foods is a very recent one in evolutionary terms. It was a great discovery of an early Homininae, and anyone now enjoy cooked salted foods. However we know that we do not need such amounts of sodium chloride in our food; it could be considered as an addiction, since, in terms of epidemiology, the present amount of salt consumption (Anonymous, 2003) is almost as bad as eating some of the toxic non-foods (pica). Accordingly, from this viewpoint, salt is a non-food.

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